

A CONTRIBUTION TO THE ODONTOLOGY
OF OREOPITHECUS

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Pp. 1-26 ; Pl. 1 : 14 Text-figures

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY

Vol. 4 No. 1

LONDON: 1959

THE BULLETIN OF THE BRITISH MUSEUM
(NATURAL HISTORY), *instituted in 1949, is
issued in five series corresponding to the Departments
of the Museum, and an Historical series.*

*Parts will appear at irregular intervals as they become
ready. Volumes will contain about three or four
hundred pages, and will not necessarily be completed
within one calendar year.*

*This paper is Vol. 4, No. 1 of the Geological (Palae-
ontological) series.*

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THE BRITISH MUSEUM

Issued April, 1959

Price Ten Shillings



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SYNOPSIS

The upper teeth of the British Museum specimen of *Oreopithecus bambolii* are described. These include the hitherto unknown Pd⁴. The wear facets on the milk-molars and molars are interpreted in terms of occlusal relations. Comparisons are made with Cercopithecidae, with fossil and Recent Pongidae and with Hominidae. It is concluded that *Oreopithecus* cannot be placed in any of these families, but is an independent derivative of a primitive catarrhine stock. Its molariform teeth show most resemblance to those of the primitive Pongidae, for example *Proconsul*, but they do not support the theory of hominid relationships. Characters shared with Hominidae, such as the shortened face and reduced canines, are probably the result of parallel evolution.

I. INTRODUCTION

THOUGH known since 1872, *Oreopithecus bambolii* Gervais, from the Pontian of Italy, has still not been fitted satisfactorily into the classification of Primates. It has been restudied in recent years by Hürzeler (1949, 1958), who has argued in favour of hominoid, rather than cercopithecoid, affinities, and has pointed out a number of resemblances to man which he believes to be significant. The British Museum possesses a specimen of *Oreopithecus*, hitherto overlooked, in which the upper dentition is very well displayed. In view of the interest aroused by Hürzeler's work, the authors decided to make a detailed study of this specimen. As a result

they have reached conclusions which diverge from those of Hürzeler, particularly in regard to the relationship between *Oreopithecus* and man.

II. THE BRITISH MUSEUM SPECIMEN

1. *Condition and identity.* The provenance of the specimen (Brit. Mus. Palaeont. Dept. M 11555) is not recorded, but the matrix is lignite, like that of other known specimens of *Oreopithecus*, and an Italian origin is reasonably certain.

The specimen consists of a palate, rather severely distorted by lateral crushing (Pl. 1). On the left side are the unerupted permanent canine, the two milk-molars, the first two molars and an unerupted third molar; P³ is partly visible above Pd³. The crown of the canine is intact; Pd³ lacks the buccal side of the crown; Pd⁴ is complete, though moderately worn; M¹ and M² are only slightly worn, but the buccal half of M¹ and the anterobuccal part of M² have been broken away; of M³ only the anterior part of the crown is preserved. On the right side the milk-molars have been removed, and the crowns of the permanent canine and P⁴ are fully preserved, but that of P³ has been broken off; M¹ and M² are severely damaged, but the unerupted M³ is fully preserved. Owing to crushing, practically no characters of the skull can be made out: the left teeth have been pushed over medially, but the right teeth still retain their original relations to the palate.

Apart from some minor differences in the arrangement of ridges, the molars closely resemble the unworn teeth of *Oreopithecus bambolii* in the Basel Museum (Hürzeler, 1949, fig. 11). Comparison with a cast of the Florence specimen, I.G.F. 4332 (Hürzeler, 1949, fig. 10) reveals differences in the measurements of the teeth (Table I), and the presence of a small metacone on P⁴, absent in the Florence specimen. These differences are probably insufficient to demand a specific distinction, and the British Museum specimen is therefore referred to *Oreopithecus bambolii*.

2. *Upper molars and milk-molars.* M³ is longer than wide, and narrower posteriorly than anteriorly. Of the four main cusps, the metacone and hypocone are less high than the paracone and protocone respectively. The apex of the paracone forms an angle of about 70° when seen in buccal view, and the metacone is equally acute.

TABLE I

(Measurements of teeth in millimetres)

<i>Oreopithecus</i>		M ³	M ²	M ¹	Pd ⁴	Pd ³ (as pre- served)	P ⁴	P ³	C
M. 11555	Length	9.4	9.0	8.2	6.6	5.5	6.5	—	7.5
	(between contact points)								
	Width	8.7	8.7	—	6.6	—	8.0	—	6.1
	(across anterior half of crown)								
I.G.F. 4332	Length	9.8	9.3	8.2	—	—	5.6	5.8	6.7
(measured on cast)	Width	9.4	8.9	7.7	—	—	9.0	8.5	6.4

The complexity of the pattern is greatly increased by the development of well-defined ridges on the slopes of the main cusps, as well as by the formation of secondary cusps and cingula, clearly indicated in Text-fig. 1. These minor features show much variability in anthropoids (Remane, 1921), and it is not surprising that Hürzeler's specimens frequently differ in details from the British Museum specimen. For example, in one of Hürzeler's specimens there is no posterobuccal cingulum, and in another the posterobuccal crest of the paracone ends at the valley between the

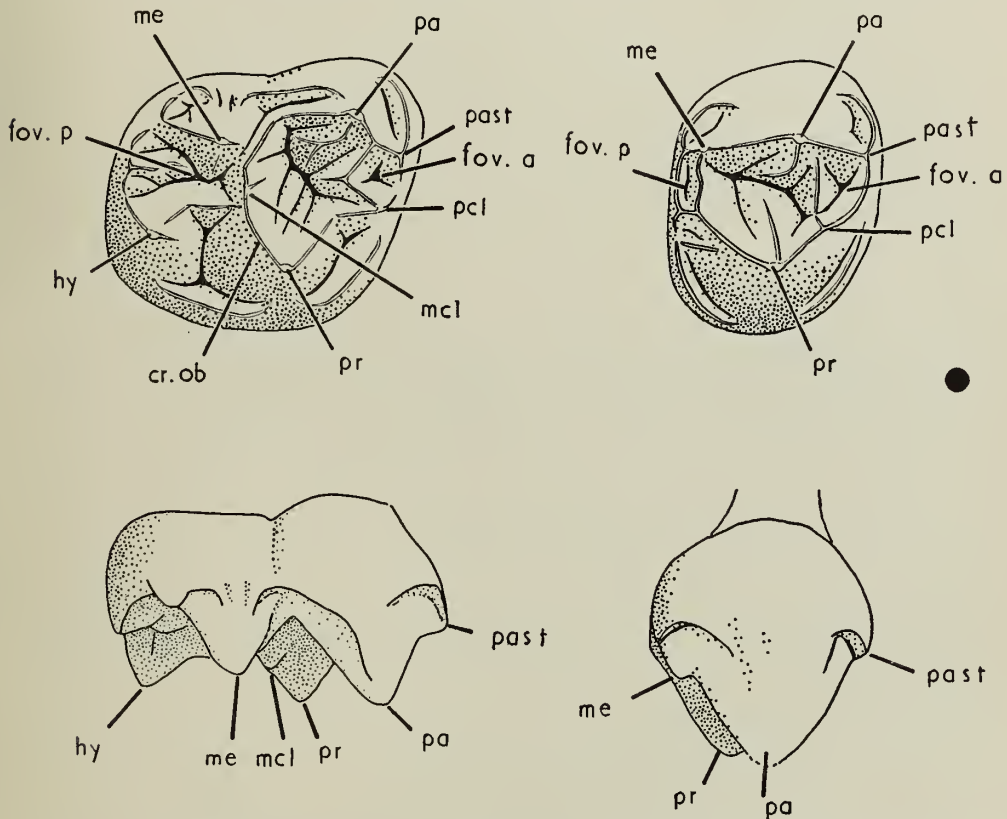


FIG. 1. *Oreopithecus bambolii* (Brit. Mus. M 11555). Crown and buccal views of right M³ and P⁴, $\times 5$. *cr. ob*, crista obliqua; *hy*, hypocone; *fov. a*, fovea anterior; *fov. p*, fovea posterior; *mcl*, metaconule; *me*, metacone; *pa*, paracone; *past*, parastyle; *pcl*, protocone; *pr*, protocone. In this and other figures ● indicates the anterior end.

paracone and metacone (Hürzeler, 1949, fig. 11). Again, in the specimens figured by Hürzeler the posterior crest of the paracone turns towards the buccal side of the crown to meet the cingulum.

There is a progressive change in the proportions of the crown as the pattern is traced forward through the molars and milk-molars (Table II; Text-fig. 2). The metacone of M² reaches a height of 2.9 mm. above the level of the buccal cingulum,

compared with 2.1 mm. on M^3 . The hypocone of M^2 is also higher than that of M^3 , reaching the same height as the protocone. The posterior crest of the paracone, which on M^3 unites with the buccal end of the crista obliqua, terminates on M^2 in a small cusp applied to the anterior side of the metacone, while the crista obliqua continues to the tip of the metacone. The fovea posterior of M^2 is divided by a crest which connects the metacone to the hypocone.

TABLE II

(Measurements in millimetres)

<i>Oreopithecus</i> (M. 11555)	M^3	M^2	M^1	Pd^4	Pd^3
Length (<i>a</i>)	9.4	9.0	8.2	6.6	5.5
Anterior width (<i>b</i>) (across paracone)	8.7	8.7	—	6.6	—
Posterior width (<i>c</i>) (across metacone)	6.8	7.8	7.8	6.5	—
Length of hypocone (<i>d</i>)	3.3	3.8	3.4	2.5	1.5
Ratios: <i>b/a</i>	0.93	0.97	—	1.00	—
<i>c/a</i>	0.72	0.87	0.95	0.99	—
<i>d/a</i>	0.35	0.42	0.41	0.38	0.27



FIG. 2. *Oreopithecus bambolii* (Brit. Mus. M 11555). Left Pd^3 - M^3 , crown view. (M^3 drawn in reverse from right side). $\times 3$.

The buccal part of M^1 is missing, but the lingual part of the tooth shows little difference from M^2 . The metaconule has become merged into the crista obliqua, and the region between the paracone and protocone is reduced in relative area and simplified.

Pd^4 has most of the elements of the molar pattern, but shows a number of distinctive features. The height of the neck of the tooth, from the cingulum to the basal margin of the enamel, is only about 2.2 mm., whereas on the molars it is about 2.7 mm. The buccal cingulum is hardly distinguishable. The posterior crest of the paracone runs to the tip of the metacone. The crista obliqua also runs to the tip of the metacone, and there is no distinct metaconule. The fovea anterior is represented by a triangular area between the anterior crest of the paracone and an anterolingual crest which diverges from it at a small angle. Comparison with M^1 and M^2 shows that the protoconule is represented by the point of junction between the anterolingual crest of the paracone and the anterior crest of the protocone. On M^3 and M^2 the posterior border of the fovea anterior is formed by a small cusp; on M^1 this cusp merges with the protoconule, and on Pd^4 it is absent. The fovea posterior of Pd^4 is divided by a crest connecting the metacone to the hypocone, as on M^1 and M^2 , but the cusp which in the molars develops on the posterior margin

of the fovea is absent in Pd⁴. The hypocone is well developed, but slightly reduced in mesiodistal diameter relatively to the protocone. As on the molars, it is connected by a crest to the crista obliqua, but in addition there is a more lingual crest, which joins the hypocone and protocone directly.

Only the lingual part of Pd³ is preserved. It does not differ significantly from the tooth described by Hürzeler (1958, fig. 14). The protocone occupies most of the lingual part of the crown, the hypocone being reduced to a small cingulum cusp. The anterolingual cingulum is narrower than on Pd⁴. At its buccal end is the parastyle, worn away to a small exposure of dentine. The protoconule appears to have merged into the crest that connects the parastyle to the protocone. A crest joins the protocone and hypocone, as on Pd⁴; running parallel to this crest, but more buccally, is the crest which connects the hypocone to the crista obliqua; more lingually there is a third crest, which passes down the posterior side of the protocone into the small cingulum basin between the protocone and the hypocone. Hürzeler's specimen shows that the metacone has merged into the posterior crest of the paracone, where it is represented by the point of junction of this crest with the crista obliqua.

3. *Permanent premolars and canine.* P⁴ is transversely oval in outline, but less transverse than in I.G.F. 4332. It is about as long as Pd⁴, but one-fifth wider. There appears to be only one buccal root. The high, acute paracone and protocone occupy almost the entire crown; the posterior part of the molar pattern is developed on the premolar to only a rudimentary extent (Text-fig. 1). There is a diminutive metacone (absent in I.G.F. 4332), connected to the protocone by a crest which represents the crista obliqua. The fovea posterior is very small, and there is no hypocone. The fovea anterior however is a relatively large triangular area, bounded by the anterior crest of the paracone and an anterolingual crest that buttresses it. The protoconule is represented by a rather indistinct elevation on the anterior marginal crest. Buccal and lingual cingula are present, broken opposite the paracone and protocone respectively, as on the molars. A short crest passes down the posterior side of the protocone into the posterior part of the lingual cingulum, corresponding to a crest found on Pd³. The central fovea is a deep basin, the floor of which sinks towards the posterior end; crests from the paracone and protocone pass down its sides.

The posterior part of left P³ is hidden by Pd³, but the anterior half of the crown is exposed and undamaged. It differs hardly at all from the corresponding part of P⁴.

The right canine is completely exposed, but the extreme tip of the cusp has been broken off. The left canine is intact, but it is visible only from the buccal and anterior sides. The base is longer than wide, as in the male canine figured by Hürzeler (1958, fig. 5), but in the proportion of height to length it resembles the female canine figured by Hürzeler (1958, fig. 6), which, however, is somewhat smaller.

No buccal cingulum is present, but there is a rather strongly developed lingual cingulum, as in the female canine described by Hürzeler. The fovea anterior is represented by a triangular groove between the anterior crest and an anterolingual crest. The more basal part of the anterior crest is accompanied on its lingual side

by a groove which appears to correspond to the much more conspicuous anterior groove of the male canine. The protocone of the premolar is represented on the canine by a slight elevation of the cingulum. More posteriorly, the cingulum widens to form a basin, corresponding to the deepest part of the central fovea of the premolar. At the posterior end, a fragment of cingulum is cut off to form the equivalent of the fovea posterior. Thus it is possible to homologise the pattern of the canine with that of the premolar (Text-fig. 3).

The premolars and canine must have erupted after M^2 . Their roots are already partly formed: the buccal root of P^4 and the root of the canine have both attained a height of about 4 mm., although the canine is placed more deeply in the jaw than the premolars. A broken section through left M^3 shows that the roots, and even the basal surface of the crown, had not developed, and therefore it seems that the milk teeth would be replaced before M^3 had erupted.

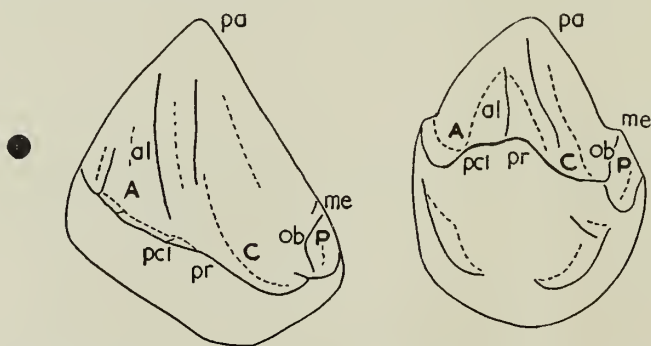


FIG. 3. *Oreopithecus bambolii* (Brit. Mus. M 11555, reversed). Left canine and P^4 , seen in lingual and slightly occlusal view. A, C, P, anterior, central and posterior foveae; al, anterolingual crest of paracone; me, metacone; ob, oblique crest; pa, paracone; pcl, protoconule; pr, protocone.

4. *Thickness of enamel.* Broken teeth show that many minor details of the pattern are represented in the dentine, the enamel forming a comparatively even layer over the crown. Using a micrometer eyepiece, measurements were made of the thickness of enamel, perpendicular to the dentine surface. On M^3 it ranged from 0.4 to 0.8 mm., on M^2 from 0.5 to 0.8 mm., and on M^1 from 0.5 to 0.7 mm. On the milk-molars the enamel is thinner, the greatest thickness found being 0.4 mm. On the premolars and canine it is about as thick as on the molars.

5. *Wear facets.* Examination of the wear facets on the milk-molars and molars by reflected light under suitable magnification shows that each facet is covered by numerous fine parallel marks. These are readily distinguished from the smaller number of scratches, usually coarser and going in various directions, due to subsequent damage to the surface; the regular scratches must have been produced by chewing movements (Butler, 1952; Mills, 1955). The positions of the facets are shown in Text-fig. 4A, where they are shaded in accordance with the direction of the scratches. It will be seen that on some facets the scratches are transverse to

the tooth row, and on others they are oblique (posterobuccal-anterolingual). Transverse scratches were produced during rotation of the mandible about the ipsilateral condyle, the lower teeth being to the buccal side of the centric position; oblique scratches were produced during rotation about the contralateral condyle, when the lower teeth were to the lingual side of the centric position (see Text-fig. 4B).

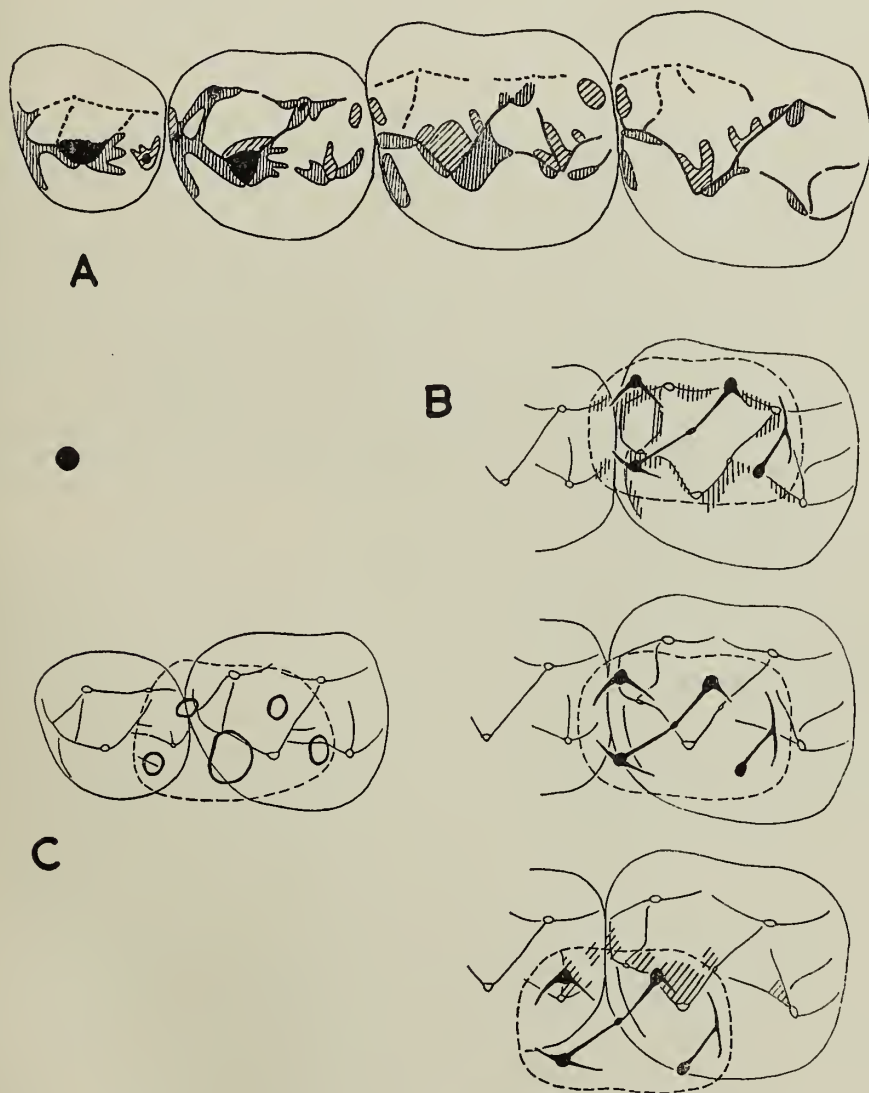


FIG. 4. *Oreopithecus bambolii* (Brit. Mus. M 11555). A, Wear facets on Pd³-M², shaded according to the direction of scratches. B, Superposition of drawings of upper and lower molars, with lower molar in extreme buccal position, in centric position and in lingual position, to illustrate the formation of the wear facets. C, Superposition of Pd₄ (after Hürzeler, 1951) on Pd³-4.

The scratches produced during transverse movement are not horizontal, but are inclined upwards towards the lingual side at a small angle (perhaps 20° : exact measurement is impossible as the orientation of the teeth is unknown). On M^2 the oblique scratches make an angle of 40° with the transverse scratches when seen in crown view; the change in direction in the vertical plane is 35° .

In the absence of the lower teeth of the same individual, the analysis which follows is based upon the structure of the lower molars in the type mandible, which is well figured by Hürzeler (1949, fig. 2), and of which the British Museum possesses a cast.

During transverse movement the lower buccal cusps (protoconid, hypoconid) passed between the upper buccal cusps (paracone, metacone), and the lower lingual cusps (metaconid, entoconid) between the upper lingual cusps (protocone, hypocone). In its most buccal position the metaconid was in contact with the lingual face of the protoconule, and as it moved lingually it wore a facet on the anterolingual cingulum, as well as on the adjacent vertical faces of the protocone and hypocone. At the same time the entoconid, passing behind the protocone, wore a notch in the crest that joins the hypocone with the crista obliqua. The crest on the lower molar which connects the metaconid with the mesoconid apparently glided across the protocone-protoconule crest of the upper molar, forming a narrow facet at its edge. A facet on the lingual face of the metacone on M^1 and M^2 appears to be due to contact with the buccal face of the small hypoconulid; a similar facet, produced by metacone-hypoconulid contact, occurs in the gorilla (Text-fig. 8). It is probable that the cuspsule on the lingual side of the paracone, on the posterior edge of the fovea anterior, made contact with the mesoconid.

In the centric position the tip of the protoconid was situated immediately to the buccal side of the protoconule, and the tip of the hypoconid was in the middle of the trigon basin. As the lower molar moved obliquely forward and lingually from the centric position, parallel to the crista obliqua, the lingual surface of the hypoconid sheared against the buccal surface of the metaconule and the protocone, and the tip of the hypoconid passed through the notch between the protocone and the protoconule. At the same time the tip of the protoconid crossed the anterior cingulum and the fovea posterior of the tooth in front, to contact the buccal slope of the hypocone. In addition to the facet on the hypocone caused in this way, there is a small facet which faces more anteriorly, apparently due to contact with the hypoconulid; it corresponds to a much larger facet present in the gorilla.

The interpretation of the occlusal relations of Pd^4 and Pd^3 is difficult because only one worn specimen of Pd_4 has been found (Hürzeler 1951), and Pd_3 is unknown. The metaconid of Pd_4 occupies a large area of the tooth and extends more posteriorly than in the molars, so that there is no distinct mesoconid, at least in the worn specimen. This large metaconid would be responsible for wear of the anterior cingulum of Pd^4 as well as that of the anterolingual side of the protocone and its anterior crest. The hypoconulid of Pd_4 is reduced, and its function of occluding with the metacone of Pd^4 has probably been taken over by the paraconid of M_1 . In other respects the occlusal relations of Pd^4 probably resemble those of the molars. The large paraconid of Pd_4 must have extended forward for some distance across

Pd³, and during transverse movement it would have passed behind the protocone of that tooth, wearing the facet on its posterior slope (Text-fig. 4B); it would thus replace the entoconid of Pd₃ which was presumably absent. The facet which covers the tip of the hypocone of Pd³ was presumably formed by the protoconid of Pd₄ during oblique movement.

Pd₃ must have been a comparatively simple tooth, possessing a metaconid or its equivalent in the form of a posterolingual crest from the protoconid. It would be responsible for wear of the anterior side of the protocone of Pd³ during transverse movements.

III. COMPARISONS

1. *Sources of material.* For comparative purposes, a study was made of specimens or casts of the upper teeth of all genera of living catarrhines and most genera of fossil forms. Extensive use was made of the collections in the British Museum (Natural History), and the authors wish to acknowledge the kind assistance given by Dr. E. I. White, F.R.S., Dr. T. C. S. Morrison-Scott, Dr. K. P. Oakley and their staff. Professor Sir Wilfrid Le Gros Clark, F.R.S. very kindly permitted them to examine specimens of *Proconsul* under his care. Thanks are also due to Dr. A. V. Stack and Dr. D. H. Goose for collections of human milk-molars.

2. *Comparison with Cercopithecidae.* The upper molar pattern of *Oreopithecus* shows little resemblance to the pattern found, with only minor variations, in all Recent Cercopithecidae and also in *Mesopithecus*. The differences may be summarised as follows:

<i>Oreopithecus</i>	Cercopithecidae
Protocone somewhat posterior to paracone.	. Protocone directly opposite paracone.
Crista obliqua strongly developed.	. Crista obliqua absent.
Protoconule and metaconule distinct.	. Conules indistinct or absent.
Cingulum well developed.	. Cingulum slight or absent.
Distinct fovea anterior.	. No fovea anterior, unless it is represented by the basin cut off by the paracone- protocone crest.
During oblique movement of the lower jaw, the tip of the hypoconid passes through the notch between the protocone and the protoconule, the hypoconid shearing against the buccal surface of the protocone.	. The tip of the hypoconid does not pass anterior to the tip of the protocone, but the plane of shear between the two cusps is rotated so as to face partly backwards in the upper molar (Mills, 1955).

Hürzeler (1949) is not convinced that the posterolingual cusp of the cercopithecoid upper molar is a true hypocone, as it is not connected with the cingulum. If it is not a hypocone, the Cercopithecidae would be far removed from the Hominoidea, which possess a true hypocone: the common origin of the two groups would have to be sought at a tritubercular stage. It would also follow that *Oreopithecus*, in which the hypocone is connected with the cingulum, is on the hominoid branch. However, an enlargement of the cusp in Cercopithecidae, in combination with a loss of the lingual cingulum, could have so altered the relations of the hypocone that its origin from the cingulum is no longer apparent. As Remane (1951) has indicated,

the less molarised forms of Pd³ show that a derivation of the cercopithecoid pattern from one more like that of hominoids is at least possible. Pd³ frequently possesses a backwardly displaced protocone and a crista obliqua, and so shows some similarity to the molars of *Oreopithecus* (Text-fig. 10). If it is assumed that these features were formerly present in the cercopithecoid molar, a distant relationship between *Oreopithecus* and the Cercopithecidae becomes feasible. In that case *Oreopithecus* would have retained on the whole a more primitive molar pattern than the Cercopithecidae (von Koenigswald, 1955).

Oreopithecus resembles most Cercopithecidae in that M¹ and M², instead of being transversely broadened teeth as in the majority of Eocene Primates, have become lengthened mesiodistally, so that the length equals or exceeds the breadth. In some living forms (*Trachypithecus*, *Presbytis*, *Presbytiscus*) the molars are still broader than long. Associated with the tendency to lengthen the molars is one, less advanced in *Oreopithecus* than in Cercopithecidae, for the posterior half of the molar to imitate the anterior half. In view of the differences of pattern it is very doubtful whether these resemblances imply relationship: they might be regarded as parallel adaptations to a herbivorous diet, found also in the Indriidae, for example. The height and sharpness of the molar cusps of *Oreopithecus* can be equalled in some Cercopithecidae, such as *Mesopithecus* and *Nasalis*. This is probably a primitive character inherited from a tarsioid ancestry.

Pd³ of Cercopithecidae (Text-fig. 10) is much longer than wide; it possesses a distinct metacone, and in most cases is almost fully molariform. This type of Pd³ is clearly specialised: in the great majority of Primates Pd³ is premolariform, with at most a rudimentary metacone. *Oreopithecus* is much nearer to the primitive condition.

The canine is comparatively small in females of Cercopithecidae, especially in some short-faced Semnopithecinae, in which its general shape is very much like that of *Oreopithecus*. A precanine diastema in the upper jaw is often absent in female Cercopithecidae (e.g. *Rhinopithecus roxellanae*, *Presbytiscus avunculus* and *Nasalis larvatus*). The male canine is distinguished from that of the female by its greater relative height and the incomplete development of its lingual cingulum, as in *Oreopithecus*. It is, however, larger and more projecting than in *Oreopithecus*, and is further distinguished in that the groove on its anterior slope is continued on to the root (Hürzeler 1958).

3. *Comparison with Pongidae*. The upper molar pattern of *Oreopithecus* is close to the pongid type. The resemblance extends to the wear facets, showing that the occlusal relations were essentially similar (Text-fig. 8). In a number of respects, however, *Oreopithecus* differs from all known Pongidae:

(1) The cusps are more acute even than in the gorilla and gibbon. This character, which is shared with a number of tarsioids and cercopithecoids, is probably primitive (Text-fig. 7).

(2) The protocone is markedly V-shaped in crown view, its tip placed near the lingual border of the crown and far removed from the protoconule, from which it is separated by a deep notch. This feature is common in early Primates and is presumably primitive (Text-fig. 5). In Pongidae the protocone and protoconule

are close together, and the arms of the protocone are more widely divergent so that the protoconule stands more immediately to the mesial side of the protocone. When the protocone is situated near the lingual border, as in living apes, the protoconule is displaced towards the lingual side of the crown (Text-fig. 6).

(3) The fovea anterior is very small, with a minimal tendency to elongate transversely to the crown. Its small size is due to the position of the protoconule quite near to the base of the paracone and to the parastyle. A similar arrangement is found in tarsioids such as *Hemiacodon* and *Necrolemuridae* (Hürzeler, 1954a : 17) and must be considered primitive. In Pongidae the fovea anterior is transversely elongated, especially in modern forms in which the protoconule is displaced away from the paracone into the lingual half of the crown (Text-fig. 5).

(4) In *Oreopithecus* there is a deep Λ -shaped groove between protocone and hypocone for the reception of the entoconid. Its anterior margin is formed by the crest joining the protocone to the metaconule; this crest is longer and directed more buccally than is normally the case in Pongidae. The posterior margin of the groove is formed by the crest which connects the hypocone to the crista obliqua near the metaconule. This crest has been regarded as a peculiarity of *Oreopithecus*, but it appears to be homologous with the "lingual marginal crest" which in Pongidae runs more directly towards the protocone, the arms of the entoconid groove having opened out (Text-fig. 5). It is probable that the condition in *Oreopithecus* is primitive in that it is associated with a markedly V-shaped protocone, well separated from the metaconule. The crest directly connecting the protocone and hypocone of Pd^4 in *Oreopithecus* is an independent formation, perhaps paralleled in the molars of Cercopithecidae.

(5) The crista obliqua, instead of passing directly to the tip of the metacone as in Pongidae, is frequently diverted in *Oreopithecus* to a cusplule situated on the antero-lingual side of the metacone. On Pd^4 , however, the crista obliqua runs to the tip of the metacone, and it is probable that this is the primitive arrangement. Hürzeler (1958) is probably correct in homologising the more buccal part of the crista obliqua with the "mesial metaconule crest" of early Primates, but its connection with the tip of the metacone appears to be a very ancient character. The condition in *Oreopithecus* would therefore constitute a peculiar specialisation, perhaps associated with the elongation of the molar.

(6) *Oreopithecus* appears to lack an occlusal facet on the posterior side of the oblique crest, produced by the hypoconulid. In the Pongidae the hypoconulid is characteristically enlarged and independent, even in the Oligocene *Propliopithecus*. While a secondary reduction is possible, it seems more likely that *Oreopithecus* is primitive in this respect.

Among the Pongidae, *Oreopithecus* shows most resemblance in the upper molar pattern to *Proconsul*, *Limnopithecus* and *Pliopithecus*. This is shown by the following characters (Text-fig. 5):

(1) Trigon basin comparatively small, owing to the vertical orientation of the cusps. This feature is also found in *Sivapithecus*. In all living Pongidae, and also in *Dryopithecus germanicus*, *D. punjabicus* and *Gigantopithecus* the trigon cusps are

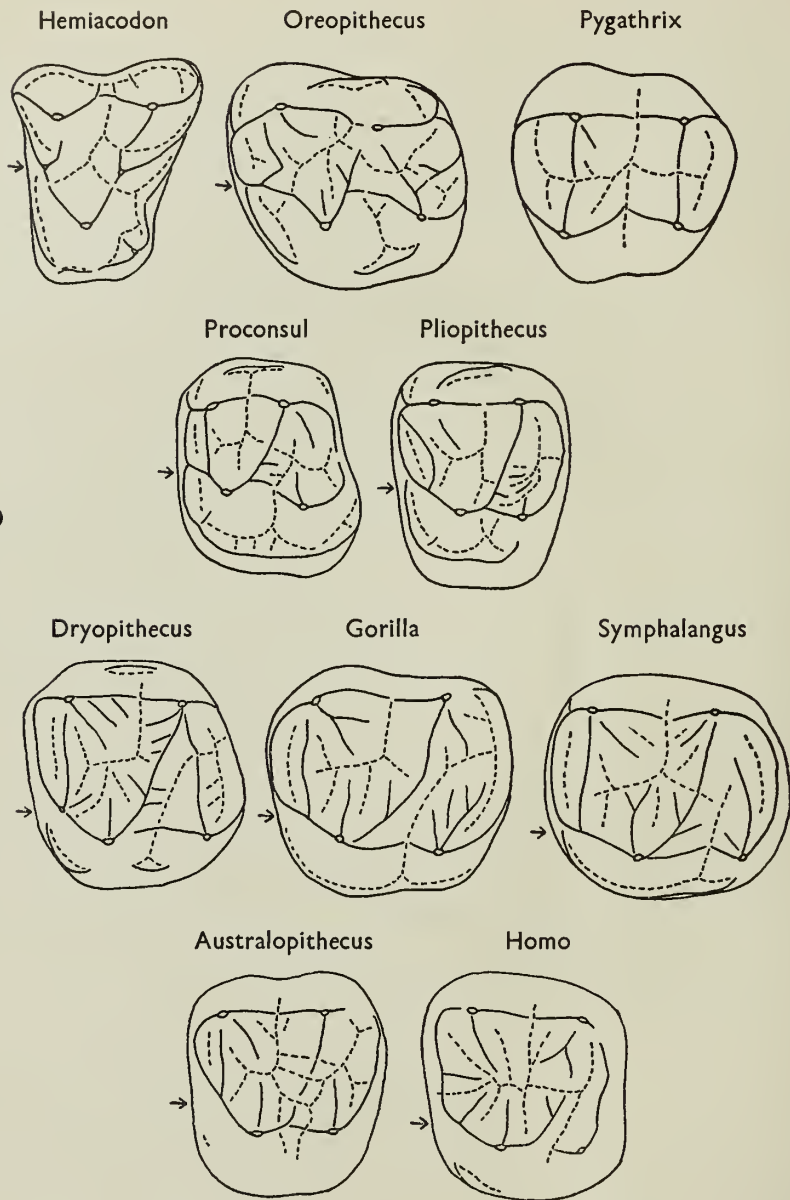


FIG. 5. Left upper molars, drawn to the same width. *Hemicacodon gracilis*, M 10386 (M¹). *Oreopithecus bambolii*, M 11555 (M² restored). *Pygathrix rubicunda*, 20.12.4.3. *Proconsul africanus*, M 14085 (M¹, reversed). *Pliopithecus antiquus*, from cast (M¹). *Dryopithecus germanicus*, from cast (M¹ or M²). *Gorilla gorilla*, 49.663 (M²). *Symphalangus syndactylus*, 19.11.12.2 (M²). *Australopithecus africanus*, from cast (M¹). *Homo sapiens*, Australian, Oxford Coll. Aus. 30.980 (M¹). The position of the protoconule is indicated by an arrow.

splayed apart, so that their tips are situated quite near the edges of the crown (Text-fig. 6).

(2) Cingulum strongly developed. In the remaining genera it is reduced to various degrees or even absent. When present the cingulum nearly always passes round the lingual side of the protocone in Pongidae, whereas in *Oreopithecus* it is interrupted there.

(3) Protoconule, when present, situated at the middle of the anterior border of the crown. Correlated with this, the fovea anterior is small and situated entirely on the buccal half of the tooth. This character occurs also in *Sivapithecus*. In

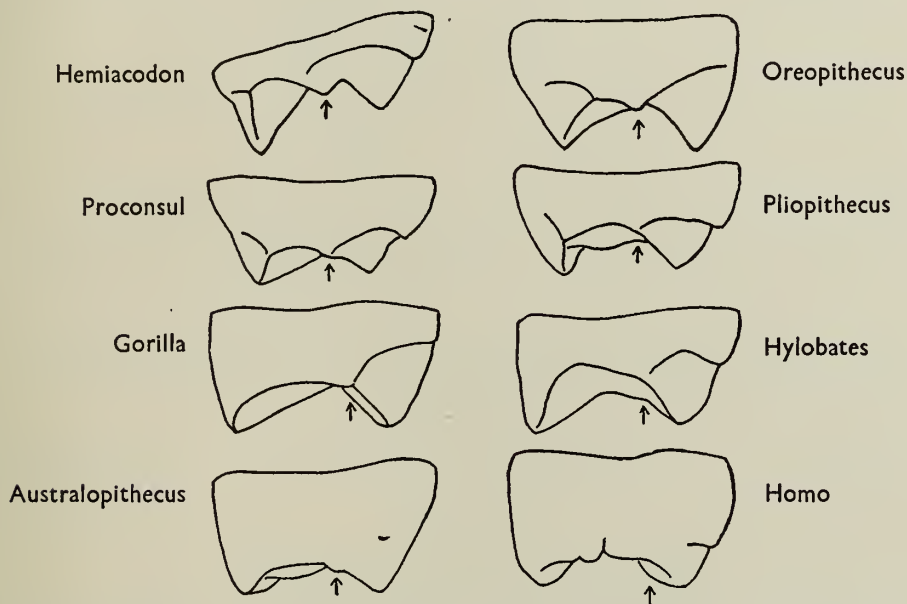


FIG. 6. Right upper molars, anterior (mesial) view. Drawn to the same width. *Hylobates hainanus*, 93.9.12.1 (M^1). *Homo sapiens*, European. Otherwise same specimens as Text-fig. 5.

Pongidae with widened trigons the protoconule is more lingually situated and the transverse diameter of the fovea anterior is greater (Text-figs. 5, 6).

(4) Paracone much higher than the parastyle, its anterior slope steeply inclined. This character is also found in the gorilla and in gibbons. At the other extreme are *Dryopithecus* and the orang (Text-fig. 7).

In its molar pattern, therefore, *Oreopithecus* appears to retain primitive features that are not known in any of the Pongidae, and at the same time it resembles what are presumably the most primitive members of the family rather than the later forms. This suggests that it is a survivor, specialised in its own way, from a prepongoid stock. Some features of the lower dentition, such as the persistence of the paraconid on M_1 , are consistent with this view.

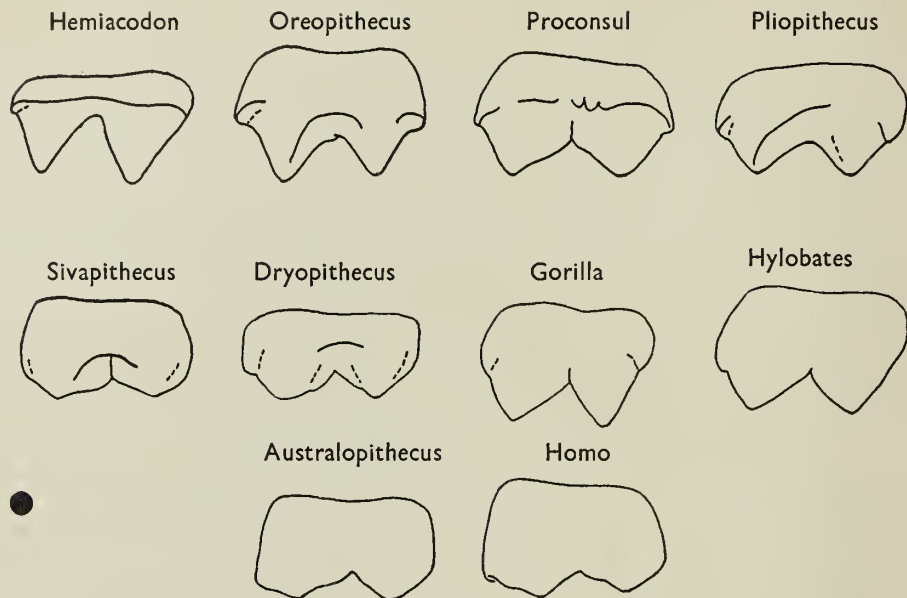


FIG. 7. Left upper molars, buccal view. Drawn to the same length. *Sivapithecus indicus*, M 13365. *Gorilla*, 61.7.29.27. *Hylobates hoolock*, 1096a (M²). *Homo sapiens*, European. Otherwise same specimens as Text-fig. 5.

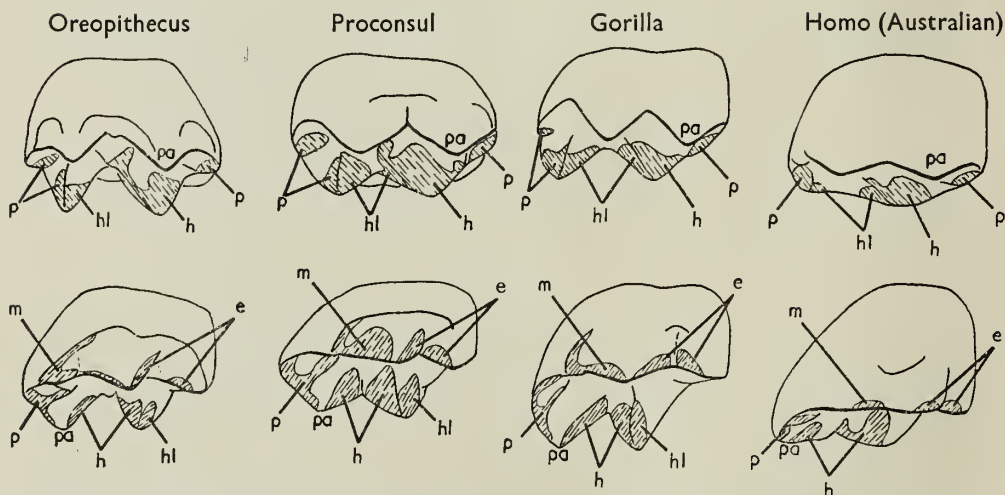


FIG. 8. Oblique views of right upper molars. Not to scale. In the upper drawings the teeth are seen in buccal and somewhat occlusal view, looking in the direction of the scratches made during the buccal phase of occlusion. In the lower drawings the teeth are seen in the direction of the oblique scratches made during the lingual phase of occlusion, i.e. anterolingually. *pa*, paracone. Wear facets due to the protoconid (*p*), hypoconid (*h*), hypoconulid (*hl*), metaconid (*m*) and entoconid (*e*) are indicated.

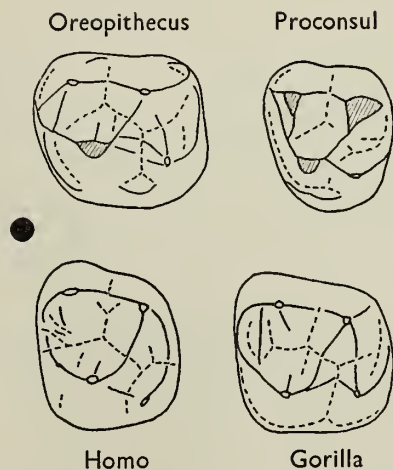


FIG. 9. Left Pd⁴, crown view. Drawn to the same width. *Oreopithecus*, M 11555. *Proconsul nyanzae*, Coryndon Museum 993, 1947. *Homo sapiens* (European), specimen supplied by Dr. M. V. Stack. *Gorilla*, 1011q.

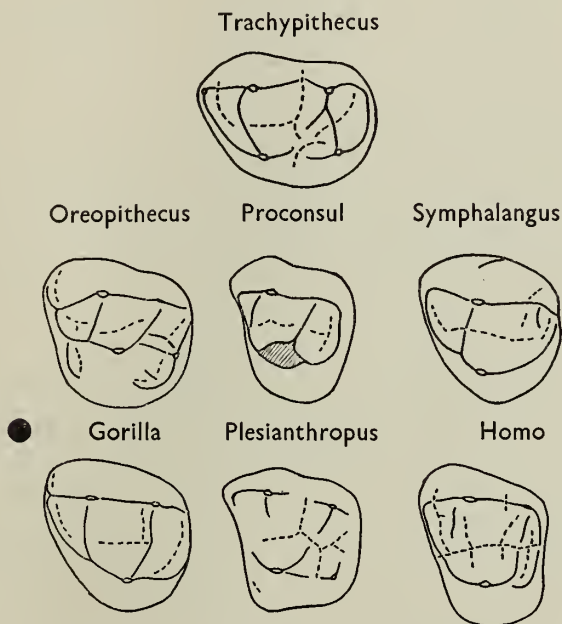


FIG. 10. Left Pd³, crown view. Scale various. *Trachypithecus obscurus*, 6.10.4.3. *Oreopithecus*, M 11555. *Proconsul nyanzae*, Coryndon Museum 993, 1947. *Symphalangus*, 0.3.2.23. *Gorilla*, 1011q. *Plesianthropus transvaalensis*, after Broom & Robinson (1950). *Homo sapiens* (European), specimen supplied by Dr. D. A. Goose.

Pd⁴ reflects the molar pattern, but in the relation of the crista obliqua to the metacone it shows a resemblance to the Pongidae that is often lost in the molars (Text-fig. 9). The level of molarisation of Pd³ is greater than in most gibbons, but is much like that of *Proconsul nyanzae* (Text-fig. 10). The characteristics of the anterior part of the molar are repeated on P⁴, as may be seen in the vertical, acute paracone, the V-shaped protocone, the small fovea anterior and the development of the cingulum (Text-fig. 11).

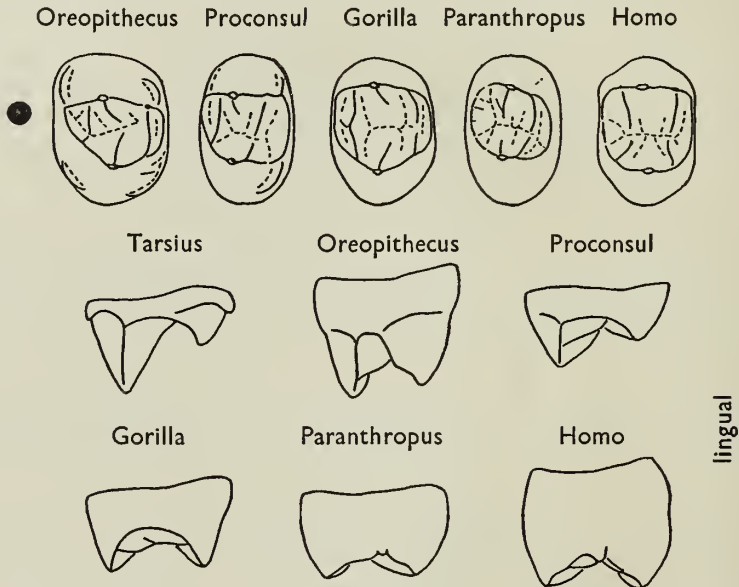


FIG. 11. Above, left P⁴, crown view. Below, right P⁴, anterior view. *Oreopithecus*, M 11555 (reversed in upper figure). *Proconsul africanus*, holotype (reversed in lower figure). *Gorilla*, 20.4.13.3. *Paranthropus robustus*, from cast (reversed in lower figure). *Homo sapiens*, specimen showing fovea anterior. *Tarsius spectrum*, 46.1.29.2.

The small size of the canine is a character shared with *Parapithecus*. Its shape is in all probability primitive (Remane, 1927, 1955) (Text-fig. 12); it shows much resemblance to the female canine of *Pliopithecus* (Hürzeler, 1954a, fig. 10). Though a precanine diastema is usually well developed in Pongidae, it is very short in the female skull of *Proconsul africanus* (Le Gros Clark & Leakey, 1951).

4. *Comparison with Hominiidae.* Hominid teeth are notoriously variable, and for considerations of space it is necessary to confine attention to those features that are sufficiently frequent to be regarded as characteristic. The material studied consisted mainly of the teeth of Europeans, Australians, *Pithecanthropus pekinensis* and Australopithecinae, the last two groups seen only as casts.

Hominid upper molars show numerous differences from those of *Oreopithecus*:

(1) They are nearly always broader than long, and thus resemble the majority of Pongidae. *Oreopithecus* is specialised in the elongation of its molars.

(2) The enamel is thick. Measurements made on broken molars of man and gorilla, comparable with those made on *Oreopithecus*, are given in Table III. The effect of the thick enamel layer is to round off the crests and cusps, so that even on unworn teeth the sulci are often more conspicuous than the positive elements of the pattern. Although there are no data for Australopithecinae, it is evident from the general appearance of their crowns that they resembled *Homo* in possessing thick enamel. Thickening of enamel would increase the life of the tooth and might be an adaptation to greater longevity in man.

TABLE III

Specimen		Maximum thickness of enamel (mm.)	Crown module	Percentage enamel thickness/module
<i>Oreopithecus</i> (M. 11555)	M ²	0·8	8·85	9·0
	M ¹	0·7	7·95 (est.)	8·8
Gorilla (23.11.29.3)	M ²	1·5	18·1	8·3
	M ¹	1·2	15·75	7·6
Orang (3.62)	M ²	1·2	13·55	8·8
	M ¹	1·2	13·75	8·7
Man (European) 3 dif- ferent individuals	M ²	1·3	9·2	14·1
	M ¹	1·3	10·5	12·4
	M ¹	1·3	9·6	13·5

(3) The cusps are very low; the paracone rises only slightly above the level of the parastyle, as in *Dryopithecus* and the orang (Text-figs. 6, 7).

(4) The trigon basin is larger than in *Oreopithecus* and primitive Pongidae, but it tends to occupy a smaller proportion of the crown area than in modern Pongidae (Text-fig. 5).

(5) There is usually no buccal cingulum. The lingual cingulum is also absent or extremely rudimentary in Australopithecinae and *Pithecanthropus*, but in *Homo* a Carabelli cingulum or cusp may develop in the neighbourhood of the protocone; it tends to extend round the lingual side of the protocone as in *Proconsul*. It is possible that the Carabelli cingulum is a new development in some races of *Homo*. Loss of cingula is probably a trend of pongid evolution.

(6) The arms of the protocone are normally widely open, as in Pongidae. The posterior arm tends to run directly backwards before turning buccally, and not infrequently it is intersected by a furrow which cuts off a small cusp behind the protocone, noticed in *Pithecanthropus* by Weidenreich (1937). It is not improbable that this cusp is the lingually displaced metaconule. A similar arrangement may be found in some oranges and chimpanzees.

(7) The groove between the protocone and the hypocone for the reception of the entoconid is shallow; the hypocone tends to be connected directly with the posterior side of the protocone, as in Pongidae.

(8) The protoconule, when differentiated, stands on the lingual half of the crown

near the protocone (see Text-figs. 5, 6 and the figure of a human molar tooth-germ by Röse, 1892). In this the Hominidae in general resemble the modern Pongidae, but *Australopithecus africanus* is more primitive in that the protoconule is near the middle line. There is a fovea anterior in this form, very similar to that of *Sivapithecus*.

(9) In most Hominidae the crest which defines the fovea anterior is incomplete, so that the fovea joins with the trigon basin. The surviving buccal part of the crest, on the slope of the paracone, develops in many cases into a small cusp. Sometimes this cusp is connected not to the paracone but to the anterior marginal crest. Here another cusplule may develop, buccal to the protoconule and in the buccal half of the crown. There is a tendency to form minor crests or wrinkles perpendicular to the anterior marginal crest. In Pongidae the union of the fovea anterior with the trigon basin is not uncommon, especially on M² and M³. It is especially frequent in the orang, which also shows the formation of wrinkles perpendicular to the anterior border. It seems more likely that the hominid fovea anterior has passed through a stage like that typical of Pongidae, than that it has been derived directly from the condition of *Oreopithecus*, as Hürzeler suggests (1958, fig. 25). Hürzeler fails to take into account the different positions occupied by the protoconule in *Oreopithecus* and in man.

(10) The hypocone is smaller than the protocone, and the fovea posterior is relatively small. This condition is usual in gibbons. There are sometimes indications of a metacone-hypocone crest, usually represented only by its two ends; the buccal end tends to branch off from the crista obliqua, giving the metacone the "clover-leaf pattern" noticed by Weidenreich (1945). Union of the buccal crest of the hypocone with the crista obliqua occurs in *Limnopithecus*.

(11) The crista obliqua is frequently broken up by one or more furrows, so that the fovea posterior becomes united with the trigon basin (Weidenreich, 1945). A similar intersection of the crista obliqua occurs in *Dryopithecus darwini* (Glaessner, 1931), and according to Remane (1921) the crista frequently fails to develop in the chimpanzee, especially on M³.

(12) When present, the crista obliqua runs to the tip of the metacone, as in Pongidae.

Thus in nearly every respect in which the hominid molar pattern differs from that of *Oreopithecus* it shows affinity to the Pongidae. Even though many of the pongid resemblances are undoubtedly the products of parallel evolution, some seem to indicate that the hominid molar has passed through a stage resembling that of primitive Pongidae. By contrast, special resemblances to *Oreopithecus* are hard to find:

(1) The cusplule which in Hominidae frequently develops lingually to the paracone, on the posterior edge of the fovea anterior, has not been observed in Pongidae. Whether it is homologous with the cusplule that develops in a similar position in *Oreopithecus* is doubtful, and little weight can be given to this resemblance.

(2) The neck of the tooth is higher than in Pongidae (Text-figs. 6, 8). This again is of little value in assessing relationships: hypsodonty is a very common adaptation in mammals to severe or prolonged wear of the teeth, and within the Pongidae the

height of the crown shows considerable variation (it is higher, for example, in *Sivapithecus indicus* than in *S. africanus*).

The milk molars and premolars, reflecting the molar pattern in various ways, repeat the distinguishing characters noted in the molars (Text-figs. 9-11). Thus Pd⁴ of Hominidae is less elongated, its cusps are blunter, the paracone and protocone are more widely separated, the cingulum is absent (except sometimes the Carabelli cingulum), and the fovea anterior is frequently united with the trigon basin. The same may be said of the premolars. Pd³ is more highly molarised in that the metacone is nearly always distinct; in *Homo* the hypocone, however, is more rudimentary than in *Oreopithecus*.

The canines differ markedly in shape (Text-fig. 12). The hominid canine is peculiar among Primates in that the basal part of the crown is elevated and the cusp is blunt and comparatively low, so that the mesial and distal shoulders, which correspond to the parastyle and metastyle of the cheek teeth, are situated relatively high on the crown (Remane, 1927). Thus the canine has become modified in the

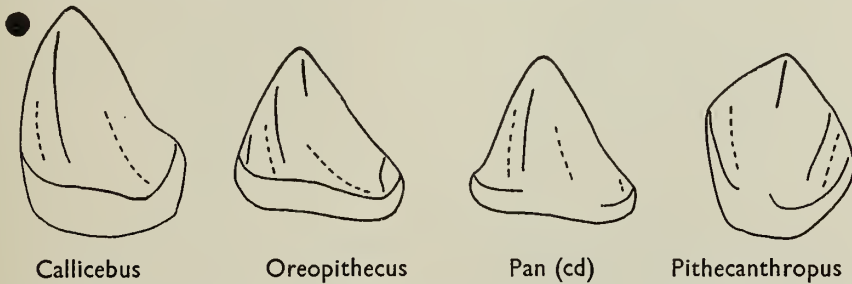


FIG. 12. Left upper canine, lingual view. Drawn to the same mesodistal length. *Callicebus leucometopa*, 27.11.1.9. *Oreopithecus*, M 11555 (reversed). *Pan*, milk canine, 48.438. *Pithecanthropus pekinensis*, from cast.

same direction as the cheek teeth. In *Oreopithecus*, as in typical Primates, the upper and lower canines are interlocking: the lower canine slides in front of the upper, producing a nearly vertical wear facet. In Hominidae the plane of contact is nearly horizontal, so that the canines meet edge to edge in the manner of incisors. In conformity with the shape of the upper canine, the embrasure between the lower canine and P₃ is very shallow in Hominidae (Text-fig. 13).

A small canine in Primates is usually associated with a short face. As the jaw swings medially, the lower canine in most Primates passes between the upper canine and I² (Text-fig. 14). When the face is long the canine can be large, for the incisors can be carried anteriorly to the upper canine so as to leave a diastema in which the lower canine can move. In short-faced Cebidae and Semnopithecinae, and probably also in *Parapithecus*, the lower canine is small enough to pass through the notch between I² and the upper canine, even though the diastema may be absent. In Hominidae the premaxilla is particularly short, and the upper incisors are situated more or less between the canines; the lower canine, instead of passing behind the incisors, travels along the incisor row. This is possible because not only has the

canine become reduced in size but its shape has been modified to permit it to bite against the edge of I^2 in the manner of an additional incisor. In *Oreopithecus* the face is also greatly shortened and the canine reduced in size, but it appears to function in a different way. To judge from I.G.F. 4332, I^2 is a reduced, conical tooth, placed at a higher level than the other teeth, and the lower canine passes below it without touching it (Text-fig. 13). Hürzeler's figure of a worn lower canine (1949, figs. 8, 9) shows a large wear facet on the posterior side, due to the upper canine, but no anterior wear which might be due to I^2 . Thus whereas both *Oreopithecus* and the Hominidae have developed to an extreme degree a common primate trend of shortening of the anterior part of the face, they have adapted the dentition to this change in different ways: *Oreopithecus* by sacrificing the canine- I^2 contact, while retaining the interlocking relation of the canines, the Hominidae by

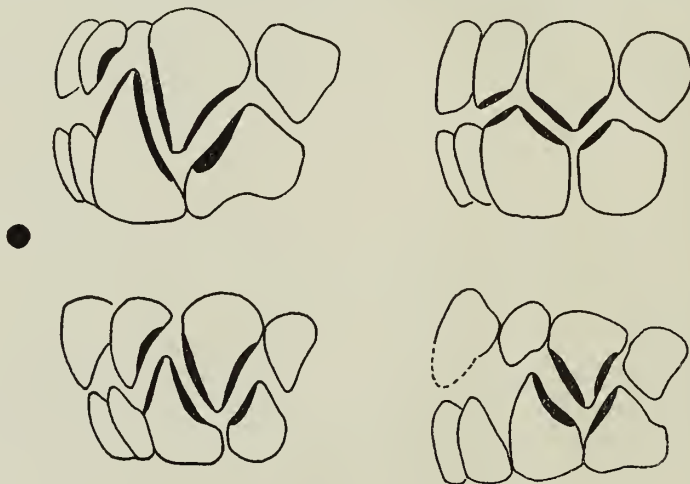


FIG. 13. Diagram to illustrate the interrelations of the anterior teeth. Position of wear facets due to upper and lower canines shown in black. Above, left, typical pongid. Above, right, hominid. Below, left, primitive primate arrangement. Below, right, *Oreopithecus*.

losing the interlocking relation and developing an incisal relation between the lower canine and I^2 .

As Remane (1955) has pointed out, the development of the metaconid on P_3 is not a character on which far-reaching phylogenetic conclusions can be based. In man this cusp is normally weaker on P_3 than on P_4 and is quite frequently very small. Its development is not closely correlated with a reduction of the upper canine, though when P_3 is specialised as a sectorial tooth the metaconid is small or absent. Its function is to extend in a lingual direction the surface which shears against the protocone of P^3 during transverse movements of the jaw. When P_3 is not highly specialised in a sectorial direction, it is not hard to conceive that the metaconid, already well developed on P_4 , could by a slight extension of the molarisation field develop also on P_3 , thus increasing the chewing surface.

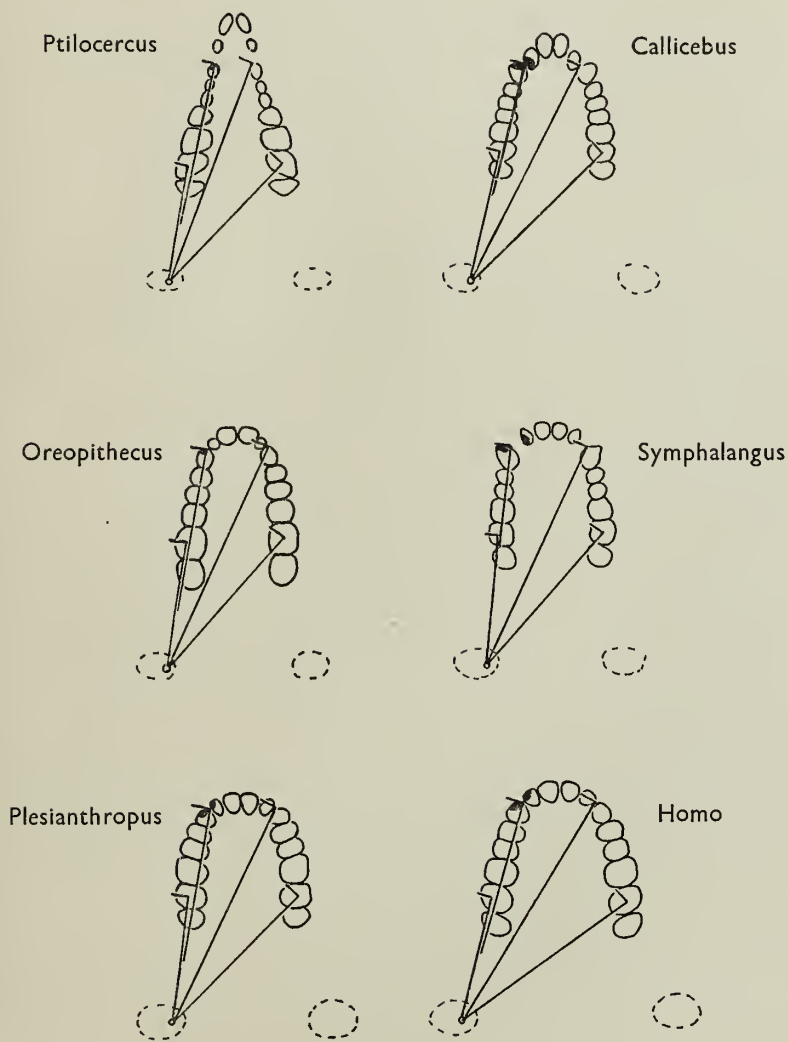


FIG. 14. Upper dental arch and position of glenoid cavities in a number of Primates, to show direction of movement of various parts of the lower dentition when the mandible rotates round a centre in the right condyle. Wear facets produced by the right lower canine are shaded. The drawing of *Oreopithecus* is a hypothetical reconstruction.

In view of the lack of other evidence for relationship, it is probable that the similarity between *Oreopithecus* and *Paranthropus crassidens* in the proportionate lengths of the teeth (Hürzeler, 1954) is mainly coincidental. The small size of the canine has already been discussed. That P_3 is shorter than P_4 is probably a correlate of the small upper canine: in Pongidae P_3 is elongated as a sectorial tooth. That M_1 is smaller than M_2 is probably a primitive character, common in Pongidae. The enlargement of M^3 and M_3 appears to be a specialisation of *Paranthropus*, paralleled not only in *Oreopithecus* but in *Proconsul nyanzae* and many Cercopithecidae.

IV. CONCLUSIONS

Hürzeler (1958) has already reviewed the various opinions on the systematic position of *Oreopithecus*, and it is unnecessary to repeat them here. As a result of the recent discovery of new material, a much more adequate knowledge of its osteology is to be expected in the near future, and no doubt a clearer picture of its relationships will emerge. The dentition however is already better known than that of most fossil Catarrhina, and while fully recognising the dangers of relying too much on a single system of organs, the authors believe that certain conclusions may confidently be drawn from its study.

Oreopithecus does not fall within the range of any of the three living families of Catarrhina. In spite of its relatively late appearance in the geological record, it possesses a number of primitive characters that it shares with tarsioids. In the upper molars these include the high crown-relief, the V-shaped protocone, the well-developed conules, the clearly differentiated cingulum, and the small fovea anterior; in the lower dentition the paraconid of M_1 and the weakly differentiated hypoconulid of M_1 and M_2 are probably primitive. At the same time *Oreopithecus* has become specialised in a number of ways: the face is very short, and the canines are probably smaller than in ancestral Catarrhina; the molars are elongated, with large hypocone and fovea posterior, and a peculiar relation of the crista obliqua to the metacone; M^3 is comparatively large, and M_3 has a well-developed "third lobe"; P^4 has only one buccal root, and P_3 has a distinct metaconid. These specialisations have presumably developed since *Oreopithecus* separated off from the common catarrhine stock.

This peculiar combination of primitive and specialised characters seems to indicate that *Oreopithecus* is the terminal form of an independent phyletic line which extended back probably into the Oligocene. Its independence would be best expressed taxonomically by placing it in a monotypic family, Oreopithecidae, as was done by Schwalbe (1916).

On the assumption that the Catarrhina is a monophyletic group, it is necessary to believe that, probably in early Oligocene time, it bifurcated into the Cercopithecoidea and Hominoidea (in the sense of Simpson, 1931), for in the early Miocene the Cercopithecidae and Pongidae were clearly distinct, and there is evidence that the separation continued back into the Oligocene. The bilophodont molar pattern of the cercopithecoids was acquired early in their evolution, while the hominoids remained more primitive in such features as the crista obliqua. In this respect

Oreopithecus falls into the hominoid group, a position which is supported by other characters of the molar pattern that it shares with the more primitive members of the Pongidae. Thus far Hürzeler (1949) may be followed.

The present study, however, gives no support to Hürzeler's further opinion (1954, 1956, 1958) that *Oreopithecus* is especially related to the Hominidae. Kálin (1955), following Hürzeler, divides the hominoids into two branches (given superfamily rank), believed to be separate since the Oligocene. The main distinguishing characters are the size of the canine, the diastema, the form of P₃ and the shape of the dental arch, all of which are related functionally to the length of the face. One would have expected *Oreopithecus* to show evidence of hominid relationship in parts of the dentition less affected by facial shortening, such as the molars, but in these the Hominidae on the contrary approach the Pongidae and differ more or less markedly from *Oreopithecus*. Even in the canine region there are differences which suggest that reduction of the canine and associated changes have taken place independently and have not followed exactly the same course in the two groups.

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PLATE 1

Oreopithecus bambolii (M 11555)

- FIG. 1. Stereophotographs of the specimen seen in palatal view. Natural size.
- FIG. 2. Left side view. $\times 2$.

1



2



1



2

